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A review of the freshwater Mollusca of Natal and their distribution

by

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SYNOPSIS

Sixty species of freshwater Mollusca occurring in Natal are listed with summaries of their distribution there and elsewhere in Africa; 10 of these are recorded from Natal for the first time. A group of species with a wide tropical range is dominant in north-eastern Natal; some of these species extend southwards over a subtraction zone. The pattern of distribution of the tropical snails supports the idea that their occurrence is largely governed by direct temperature effects. Tropical forms living unusually far south occur in isolated populations. There are also some species in Natal characteristic of temperate parts of southern Africa, as well as ubiquitous species. The occurrence in the continents of the southern hemisphere of mutelid mussels and *Ferrissia* (*Pettancylus*) seems explicable by a northern origin.

INTRODUCTION

Natal Province occupies an area of approximately 80,000 km² (31,000 sq. miles) of the coastal region of eastern South Africa between latitudes 27° and 31°, including the territories known as Zululand and Tongaland. Physical boundaries are provided to the east by the Indian Ocean and to the west by the Drakensberg escarpment, but ecological conditions at the northern and southern boundaries of the province respectively are similar to those in adjacent parts of Mocambique and Eastern Cape Province.

The climate is in general of the 'wet summer' type (Niddrie, 1951) with a transition in the north east towards the tropical climate of Mozambique. According to the system of climato-ecological regions proposed by Van Zinderen Bakker (1962) the greater part of Natal is within the semi-arid tropical region, and the extreme south and west lie in the semi-arid warm temperate region. The isopleths of the climatic elements run approximately parallel to the Drakensberg escarpment, deviating where mountainous spurs project eastwards and where valleys of major rivers cut deeply into the land surface; one consequence in the colder months of the year is the extension inland from the coast of warm conditions up the river valleys, an effect which is particularly marked in the basin of the Tugela River (Niddrie, *loc. cit.*).

Some freshwater molluscs occur in saline estuarine waters and other snails which prefer saline conditions may occasionally be found in fresh waters. There may, therefore, be difficulties in deciding which of these euryhaline species should be included in a discussion of a freshwater fauna. The present list includes forms which occur usually in fresh water but may also inhabit somewhat saline water, according to the author's experience and observations described in the literature; these forms belong to the genera *Melanoides*,

Thiara, *Neritina*, *Tomichia*, and *Septaria*. Forms such as *Assiminea bifasciata* Nevill which occur in estuarine lagoons of low salinity but apparently do not inhabit fresh inflowing streams are omitted from the present list, as is the genus *Succinea* which is predominantly terrestrial although some species are associated with emergent aquatic vegetation.

Forty six forms of freshwater Mollusca were listed for Natal by Connolly (1939); additional forms have been recorded by Mandahl-Barth (1958 & 1960), Kuiper (1964), Van Eeden & Brown (1966), and Kuiper (1966). A further 10 forms are recorded in the present paper bringing the total to 60 allowing for 2 cases of synonymy among those recognised by Connolly. Knowledge of variation in the shell and anatomy of nominal species occurring in Natal, and in southern Africa as a whole, is incomplete and some changes in taxonomic status are to be expected in future revisions. It seems worthwhile, nevertheless, to attempt a biogeographical analysis of the known forms and present information which may be compared with that available for some other groups of animals in southern Africa (Balinsky & Rowan, 1962). Natal comprises an area of particular interest containing the southern limits of many freshwater and terrestrial molluscs, fishes (Crass, 1964), Amphibia (Poynton, 1964), and other organisms which may be considered to be members of the tropical fauna.

New information given in this paper is derived from collections made by the author from 1964-5 in the course of an investigation into the distribution of potential intermediate hosts of bilharziasis. The investigation forms part of a survey of the freshwater Mollusca of the whole of South Africa from which records are collated in the Potchefstroom Division of the Bilharzia Research Group of the Council for Scientific and Industrial Research, and it is intended that distributions should be described in detail in future publications. Distributions are therefore summarised in the present paper and details of localities are given only when of particular interest. Material has been deposited in the Experimental Taxonomy Section of the Zoology Department, British Museum (Natural History), and in the Institute for Zoological Research, University of Potchefstroom; numbers of samples in the collection of the latter institution are prefixed by the letters IZP.

The author is indebted to Mr. J. G. J. Kuiper for identifying species of *Pisidium* and *Eupera*, to Dr. G. Mandahl-Barth for identifying other lamellibranchs, and to Dr. R. Elsdon-Dew for accommodation in the Institute for Parasitology, Durban from November, 1963 to July, 1965.

FRESHWATER MOLLUSCA RECORDED FROM NATAL

Cases of synonymy recognised by Connolly (1939) and followed in the present list concern the following forms described from Natal: *Lymnaea umlaasiana* Küster, *Planorbis leucochilus* Melville & Ponsonby, *Physa zuluensis* Melville & Ponsonby, *Spatha natalensis* Lea, and *Corbicula natalensis* Clessin. Two cases of synonymy proposed by other authors are recognised here among forms listed as distinct by Connolly: *Lymnaea caillaudi* = *L. natalensis*, and *Cafferia connollyi* = *C. caffer*. New localities in Natal are given only when they provide a significant addition to the information given by Connolly (1939). 'Cape Province' is used without qualification when a form occurs in the western and eastern regions.

Class *GASTROPODA*

Subclass *PROSOBRANCHIA*

Lanistes Montfort

Lanistes ovum Troschel, 1845. Tette, Mozambique

Distribution in Natal: Pongola River (Connolly, 1939); Tete Pan (*leg.* Brown 57, IZP 64.1.66).

Range: South eastern Transvaal (Schutte & Frank, 1964); Mozambique (Azevedo et al., 1961); Angola (Wright, 1963 a); Congo (Pilsbry & Bequaert, 1927); southern Kenya (Haas, 1936).

Bellamya Jousseaume

Bellamya capillata (Frauenfeld, 1865). Lake Nyasa

This form is probably synonymous with *B. unicolor* (Olivier) described from Egypt.

Distribution in Natal: Lake Sibayi (Connolly, 1939); Tete Pan (*leg.* Brown, 57, IZP 64.1.66)

Range: South eastern Transvaal (Schutte & Frank, 1964); Mozambique (Azevedo et al., 1961); *B. unicolor* is widely distributed in Africa northwards to Egypt.

Cleopatra Troschel

Cleopatra ferruginea (Lea, 1850). Zanzibar

Distribution in Natal: Manuan Creek and Otolini* district (Connolly, 1939); Tete Pan (*leg.* Brown 57, IZP 64.1.66); stream near north end of Lake St. Lucia (*leg.* Brown, 408, IZP 64.2.66).

Range: South eastern Transvaal (Schutte & Frank, 1964); Mozambique (Azevedo et al., 1961); Tanganyika (Mozley, 1939); Somalia (Connolly, 1928). A record from Prieska, Cape Province is cited by Connolly (1939) thus, '*leg.* Gibbons *fide* Melville & Ponsonby'.

Thiara Röding

Thiara vouamica Bourguignat, 1889

Distribution in Natal: Coastal localities as far south as Ifafa (Connolly, 1939).

Range: Eastern coast of Africa northwards to Somalia (Connolly, *loc. cit.*).

Melanoides Olivier

Melanoides tuberculatus (Müller, 1874). Coromandel, India

Distribution in Natal: Estuarine lagoons and freshwaters near the coast as far south as the Umzimai River, north of Port Shepstone (*leg.* Brown, 282, IZP 64.3.66). The most inland locality known is a tributary of the Riet River, Pongola (*leg.* Brown, 290, IZP 64.4.66).

Range: South eastern Transvaal (Schutte & Frank, 1964); Mozambique (Azevedo et al.,

* Possibly a mispelling of Otobotini.

1961); Angola (Wright, 1963 a); northwards in eastern Africa to the Mediterranean and Asia. A record of *M. victoriae* (Dohrn) from near Port Elizabeth is given with implied reservation by Connolly (1939) thus, '*fide* Crawford !!'; it seems likely that this record refers to an isolated population of *M. tuberculatus* rather than *M. victoriae* which is otherwise known in South Africa only from the eastern Transvaal.

Tomichia Benson

Tomichia natalensis Connolly, 1939. Lower Umkomaas, Natal

Distribution in Natal: Winkel Spruit (Connolly, 1939); Inyezane and Ibati Rivers between Empangeni and Gingindlovu (*leg.* Brown, 383 & 384, IZP 64.5.66 & 64.6.66).
Range: The genus *Tomichia* is characteristic of southern Cape Province and *natalensis* is the most northerly occurring of this group of forms. The genus is otherwise known only from the Congo (Verdcourt, 1951).

Neritina Lamarck

Neretina natalensis Reeve, 1885. Umgeni River, Natal

Distribution in Natal: Coastal localities as far south as the Umzimkulu River (Connolly, 1939); Umlalazi River (*leg.* Brown, 387, IZP 64.7.66).
Range: Mozambique and northwards to the Pangani River, Tanganyika (Pilsbry & Bequaert, 1927).

Neritina gagates Lamarck, 1822

Distribution in Natal: Tongaat, Umkomaas, Umgeni lagoon (Connolly, 1939).
Range: Mascarene and Seychelle Islands (Germain, 1921).

Septaria Ferrusac

Septaria tessellaria (Lamarck, 1816)

Distribution in Natal: Coastal localities between Amanzimtoti and the Umkomaas River (Connolly, 1939).
Range: Ceylon and the Philippine Islands (Connolly, *loc. cit.*).

Subclass *PULMONATA*

Physa Draparnaud

Physa acuta (Draparnaud, 1805)

Distribution in Natal: Durban district between Mhlatuzane River and Stanger, and inland near New Hanover (*leg.* Brown, 98, IZP 64.8.66).
Range: South western Europe and Egypt (Ehrmann, 1953). It is possible that forms of *Physa* occurring in eastern Africa (Mandahl-Barth, 1962) and Ethiopia (Brown, 1965) may be *P. acuta*. Van Bruggen (1966) believes that this species may have been introduced into South Africa from Europe.

Lymnaea Lamarck

Lymnaea natalensis Krauss, 1848. Natal

L. caillaudi Bourguignat, 1883. Lake Tana, Ethiopia. Synonymous with *natalensis* according to Hubendick (1951).

Distribution in Natal: Widely distributed from sea level to the foothills of the Drakensberg escarpment (van Eeden et al., 1965).
Range: This species includes a large number of named forms (Hubendick, *loc. cit.*) distributed in Africa between Cape Province and Egypt, and in the Arabian Peninsula.

Lymnaea truncatula (Müller, 1774)

Limnaeus umlaasianus Küster, 1862. Umlaas River, Natal.

Distribution in Natal: Umlaas River and coastal localities in the Durban district (Connolly, 1939); Pietermaritzburg (*leg.* Cawston, Natal Museum); Bushmans River at Estcourt (*leg.* Brown, 488, IZP 64.10.66).
Range: Cape Province and eastern Transvaal where it is rare in comparison with other *Lymnaea* species (van Eeden et al., 1965); Kenya (Hubendick, 1951; Mandahl-Barth, 1954); Ethiopia (Brown, 1965); Western Aden Protectorate (Wright, 1963 b); widely distributed in the Palearctic region.

Lymnaea columella Say, 1817. Philadelphia, North America

Distribution in Natal: Widely distributed and abundant, particularly in the central part of the province (van Eeden & Brown, 1966); at 1,600 m (5,250 ft.) near Sani Pass Hotel (*leg.* Brown, 529, IZP 64.11.66).
Range: This species has become abundant in large areas of Cape Province and Transvaal; it was first recorded at Jonkershoek Fish Hatchery, western Cape Province in 1944 (Barnard, 1948). Rhodesia (Mandahl-Barth, 1962).

Biomphalaria Preston

Biomphalaria pfeifferi Krauss, 1848. Umgeni Valley, Natal

Distribution in Natal: Most abundant near the coast, occurring furthest inland in the Umgeni River system north of Pietermaritzburg (van Eeden et al., 1965).
Range: Eastern Cape Province and Transvaal (van Eeden et al., *loc. cit.*); widely distributed in Africa northwards to Ethiopia (Brown, 1965); Western Aden Protectorate (Wright, 1963 b, as *B. rueppelli*).

Biomphalaria angulosa Mandahl-Barth, 1957. Lake Ngwasi, Tanganyika.

Distribution in South Africa: Durban and Johannesburg (Mandahl-Barth, 1958).
Range: Northern Rhodesia (Mandahl-Barth, *loc. cit.*).

Van Eeden (1966) believes this species to have been introduced into South Africa, where it has apparently become extinct in the recorded localities.

Gyraulus Charpentier

Gyraulus costulatus Krauss, 1848. Umgeni Valley, Natal.

Distribution in Natal: Common in the eastern region but becoming rare in the west where the most inland localities known are Umzimkulu (*leg.* Brown, 391, IZP 64.12.66) in the south, and Hattingspruit Dam near Dundee in the north (*leg.* Brown, 40, IZP 64.13.66).
Range: Eastern Cape Province (14 miles north east of Kei Mouth, *leg.* van Eeden, IZP 105.3.59); Transvaal except for some high altitude areas (Brown, in preparation); Mozambique (Azevedo et al., 1961); widely distributed in Africa northwards to Ethiopia (Brown, 1965).

Gyraulus lamyi (Germain, 1908). Lake Tanganyika.

Distribution in Natal: The higher altitude region west of a line through Port Shepstone, Greytown, Dundee, and Piet Retief (Brown, in preparation). It seems likely that the record by Connolly (1939) from near the coast at Reunion may refer to an unusually elevated shell of *G. costulatus*.
Range: Cape Province, Free State, and Transvaal (Brown, *loc. cit.*); otherwise recorded only from the type locality.

Anisus Studer

Anisus natalensis (Krauss, 1848). Umgeni Valley, Natal

Planorbis leucochilus Melville & Ponsonby, 1903. Killarney Lake, Pietermaritzburg.

Distribution in Natal: Common over the greater part of the province (Connolly, 1939; Brown, in preparation).
Range: Cape Province, Free State, Transvaal (Connolly, loc. cit.); Mozambique (Azevedo et al., 1961); Uganda, Tanganyika (Mandahl-Barth, 1954); Ethiopia (Brown, 1965).

Anisus anderssoni (Ancey, 1890). Ovambonde, South West Africa

Distribution in Natal: Durban district, Mooi River (Connolly, 1939).

Range: Cape Peninsula, Transvaal, Mozambique (Connolly, *loc. cit.*). Some or all records of this species may refer to that following.

Anisus coretus (de Blainville, 1826). Podor, Senegal

Distribution in Natal: Mhlangana River near Durban (*leg.* Brown, 68, IZP 64.15.66); Ngoboseleni Lake near Sordwana Bay (*leg.* Brown & Oberholzer, IZP 62.13.66).
Range: Cameroon (Wright, 1965); Ethiopia (Brown, in press). This species is similar to a small specimen of *A. natalensis* but shows clear anatomical differences to that species. The anatomical study of small specimens of *Anisus* will probably reveal that *A. coretus* is widely distributed.

Segmentorbis Mandahl-Barth

Segmentorbis planodiscus (Melville & Ponsonby, 1897). Umgeni Valley, Durban

Distribution in Natal: Localities near the coast between Umbogintwini and the Mtubatuba district (*leg.* Brown, 412, IZP 64.16.66).

Range: Eastern Cape Province, Ovamboland (Connolly, 1939); south eastern Transvaal (Schutte & Frank, 1964). Specimens from Uganda tentatively identified as *planodiscus* by Mandahl-Barth (1954) are *angustus* according to the same author (pers. comm., 1965).

Segmentorbis angustus (Jickeli, 1874). Mekerka, Ethiopia

Distribution in Natal: Localities near the coast between the Makosi River, 10 miles north of Port Shepstone (*leg.* Brown, 323, IZP 64.17.66) and the Inyezane River, north of Gingindlovu (*leg.* Brown, 383, IZP 64.18.66).

Range: Mozambique (Azevedo et al., 1961); eastern Africa (Mandahl-Barth, 1954); Congo (Pilsbry & Bequaert, 1927); Cameroon (Wright, 1965); Ethiopia (Brown, 1965).

Segmentorbis kanisaensis (Preston, 1914). Kanisa, Sudan

Distribution in Natal: Merebank near Durban (Connolly, 1939); Lake in Happy Valley Reserve at Merebank (*leg.* Brown, 500, IZP 64.19.66); Ngoboseleni Lake near Sordwana Bay (*leg.* Brown & Oberholzer, IZP 62.13.66).

Range: Eastern Transvaal (Oberholzer & van Eeden, in press). *S. kanisaensis* has been recorded from widely separated localities as far north as Gambia (Smithers, 1956) and Ethiopia (Brown, 1965).

Lentorbis Mandahl-Barth

Lentorbis junodi (Connolly, 1925). Rikatla, Mozambique

Distribution in Natal: Localities near the coast as far south as the Mhlangana River near Durban (*leg.* Brown, 68, IZP 64.15.66).

Range: Mozambique (Azevedo et al., 1961); eastern Africa (Mandahl-Barth, 1954); Ethiopia (Brown, 1965).

Lentorbis carringtoni (Azevedo *et al.*, 1961). Nacala, Mozambique. **New combination**

Distribution in Natal: Tributary of Umgeni River near Durban (*leg.* Brown, 163, IZP 64.20.66).

Range: Eastern Transvaal (Oberholzer & van Eeden, in press); Mozambique, between Manhica and the Komati River (*leg.* Brown, 466, IZP 64.21.66).

Helisoma Swainson

Helisoma sp.

Many shells were obtained from a concrete-lined pond at Mandini Paper Mill (*leg.* Brown, 508, IZP 64.22.66) together with *Biomphalaria pfeifferi* and *Lymnaea columella.* Living *Helisoma* had previously been sufficiently abundant to impede the flow of water from the pond through filters, but treatment with copper sulphate had apparently killed the entire population.

Bulinus Müller

The synonymy of *Bulinus diaphanous* and *B. corneus* with *B. tropicus* was proposed by Mandahl-Barth (1958); at present many intricate taxonomic problems within the genus *Bulinus* remain to be solved and for this reason these forms are listed separately overleaf.

Bulinus (*Bulinus*) *natalensis* (Küster, 1841). Umgeni Valley, Natal

Physa zuluensis Melville & Ponsonby, 1903. Eastern Zululand.

Distribution in Natal: The coastal area from Durban northwards (Connolly, 1939; Brown et al., in press, as the *B. natalensis* group).

Range: Eastern Transvaal, South West Africa, Rhodesia, Zambia, Angola, Congo, Tanganyika (Mandahl-Barth, 1965). Although Mandahl-Barth includes *B. depressus* Haas in the synonymy of *natalensis* it is possible that they are distinct and both species may occur in Natal (van Eeden et al., 1965).

Bulinus (*Bulinus*) *tropicus* (Krauss, 1848). Lepenula River, Transvaal

Distribution in Natal: Widely distributed but less frequent near the coast in the central and northern regions where the *B. natalensis* group occurs.

Range: Cape Province to northern Transvaal (van Eeden et al., 1965); Northern and Southern Rhodesia (Mandahl-Barth, 1958); Mozambique (Azevedo et al., 1961); Cameroon (Wright, 1965).

Bulinus (*Bulinus*) *diaphanous* (Krauss, 1848). Umgeni Valley, Natal

Distribution: Umgeni Valley, Cape Province, Damaraland (Connolly, 1939).

Bulinus (*Bulinus*) *corneus* (Morelet, 1889). Port Elizabeth, Cape Province

Distribution: Mooi River in Natal, Cape Province, Free State, Damaraland (Connolly, 1939)

Bulinus (*Bulinus*) *forskali* (Ehrenberg, 1831). Damietta, Egypt

Distribution in Natal: Widely distributed in the east up to an altitude of 1,360 m (4,500 ft.) east of Mooi River town.

Range: Cape Province northwards in eastern Africa to the lower Nile and also widely distributed in western Africa.

Bulinus (*Physopsis*) *africanus* (Krauss, 1848). Port Natal

Distribution in Natal: In the eastern region particularly near the coast, occurring inland at Pietermaritzburg (*leg.* Brown, 91, IZP 64.25.66), and in the Tugela River basin at Colenso and Newcastle (*leg.* Brown, 195, IZP 64.26.66).

Range: Eastern Cape Province, south westwards to the Humansdorp district (van Eeden et al., 1965); eastern Transvaal (Schutte & Frank, 1964); Mozambique (Azevedo et al., 1961); widely distributed in eastern Africa northwards to Ethiopia (Brown, 1965).

Bulinus (*Physopsis*) *globosus* (Morelet, 1866). Rio Dande, Angola

Distribution in Natal: North eastern coastal plain (Brown, 1966); Lake Futululu and near Lake Nhlabane, Richards Bay district (*leg.* Brown & Oberholzer, IZP 83.20.66).

Range: South eastern Transvaal (Schutte & Frank, 1964); Mozambique (Azevedo et al., 1961); widely distributed in eastern and western Africa northwards to the Sahara (Mandahl-Barth, 1958).

Burnupia Walker

A revision of this genus would probably reveal cases of synonymy among the large number of nominal forms recognised by Walker (1923) and Connolly (1939). These limpets are common in the freshwaters of Natal, usually occurring on stones in rapidly flowing water but also on vegetation in pools and lakes (e.g., Lake Sibayi. *leg.* Brown 61, IZP 64.27.66). Specific identification of recently collected material has not been attempted and localities given by Connolly are summarised below.

Burnupia caffra (Krauss, 1848). Pietermaritzburg, Natal

Distribution: Durban and Pietermaritzburg areas, Cape Province (Connolly, 1939); Congo (Pilsbry & Bequaert, 1927); Ethiopia (Brown, 1965).

Burnupia gordonensis (Melville & Ponsonby, 1903). Gordon Falls, Natal

Distribution: Durban and Pietermaritzburg areas, eastern Cape Province (Connolly, 1939); Angola (Wright, 1963 as c.f. *gordonensis*).

Burnupia stenochorias (Melville & Ponsonby, 1903). Ebb and Vloed, eastern Cape Province

Distribution: Durban area, eastern Cape Province, Free State (Connolly, 1939).

Burnupia brunnea Walker, 1923. Zoutpansberg, Transvaal

Distribution: Dargle and other localities in the Umgeni River system (Connolly, 1939).

Burnupia nana Walker, 1923. Karkloof Stream, Natal

Distribution: Pietermaritzburg district, Pretoria (Connolly, 1939).

Burnupia farquhari Walker, 1923. York, Cape Province

Distribution: Bulwer in Natal (Connolly, 1939).

Burnupia ponsonbyi Walker, 1923. Umgeni River, Natal

Distribution: Pietermaritzburg district and Mooi River, Natal (Connolly, 1939).

Burnupia capensis natalensis Walker, 1923. Umhlatuzani River at Malvern, Natal

Distribution: Coastal region of Natal from Oribi Flats northwards to Eshowe (Connolly, 1939).

Burnupia obtusata Walker, 1926. Pietermaritzburg, Natal

Distribution: Known from type locality only.

Ferrissia Walker

A revision of this genus would probably establish many cases of synonymy among the nominal forms. *Ferrissia* spp. occur in the greater part of the province, usually on vegetation in still or slowly flowing waters. Specific identification of recently collected material has not been attempted and localities given by Connolly (1939) are summarised below.

Ferrissia burnupi (Walker, 1912). Equeefa, Natal

Distribution: Coastal region of Natal between Equeefa and Durban area, Pietermaritzburg, Pretoria (Connolly, 1939); south eastern Transvaal (Schutte & Frank, 1964); Tanganyika (Mozley, 1939).

Ferrissia connollyi (Walker, 1912). Black River near Capetown

Distribution: Umbilo River at Sarnia in Natal, eastern and western Cape Province (Connolly, 1939).

Ferrissia fontinalis (Walker, 1912). Randjesfontein, Transvaal

Distribution: Durban district, Free State, western Transvaal (Connolly, 1939).

Ferrissia natalensis Walker, 1923. South Coast Junction, Natal

Distribution: Durban (Connolly, 1939).

Ferrissia equeefensis (Walker, 1912). Equeefa, Natal

Distribution: Known only from type locality.

Ferrissia clifdeni Connolly, 1939. Umtwalumi near Port Shepstone, Natal

Distribution: Malvern in Natal, Mooi River at Potchefstroom (Connolly, 1939).

Class *LAMELLIBRANCHIA*

Cafferia Simpson

Cafferia caffer caffer (Krauss, 1848). Natal

Unio (*Cafferia*) *connollyi* Pilsbry, 1923. Port Natal. Synonymous with *caffer* Krauss according to Haas (1936).

Distribution in Natal: Umpingave River, Msunduze River at Pietermaritzburg (Connolly,

1939); Black Umfolozi River (Haas, 1936); Horn River near Newcastle (*leg.* Brown, 194, IZP 64.28.66).
Range: Cape Province northwards to Southern Rhodesia (Connolly, 1939).

Caelatura Conrad

Caelatura framesi (Connolly, 1925). Near Premier Mine, Pretoria

Distribution in Natal: Tete Pan (*leg.* Brown, 57).
Range: Eastern Transvaal (Haas, 1936); Mozambique (Connolly, 1939).

Aspatharia Bourguignat

Aspatharia wahlbergi (Krauss, 1848). Aapies River, Transvaal

Spatha natalensis Lea, 1864. Umpingave River, Natal.

Distribution in Natal: Enseleni River (Connolly, 1939); Msunduzi River south of Mtubatuba (*leg.* Brown, 509).
Range: South eastern Transvaal (Schutte & Frank, 1964); northern Transvaal, Ovamboland, Bechuanaland, Southern Rhodesia, Mozambique (Connolly, 1939); Ethiopia (Connolly, 1928).

Corbicula Megerle von Mühlfeld

Corbicula africana (Krauss, 1848). Gauritz River, Cape Province

Corbicula natalensis Clessin, 1877. Natal.

Distribution in Natal: In the eastern region, particularly near the coast as far south as the Ifafa River (*leg.* Brown, 321, IZP 64.30.66). The furthest record inland is from the Umgeni River at Nagle Dam (*leg.* Brown, 89, IZP 64.29.66).
Range: Eastern and western Cape Province northwards to east African great lakes (Connolly, 1939).

Sphaerium Scopoli

Sphaerium capense (Krauss, 1848). Knysna River, Cape Province

Distribution in Natal: Western shore of Lake St. Lucia (Haas, 1936); Wewe River at Tongaat (*leg.* Brown, 345, IZP 64.31.66); Lake Futululu and small lake 4 miles south east of Empangeni (*leg.* Brown & Oberholzer, IZP 83.15.66 & 83.29.66).
Range: Southern Rhodesia (Connolly, 1939); Congo (Haas, 1936).

Pisidium C. Pfeiffer

Pisidium pirothi, Jickeli, 1881. Harasa, between Atbara and Bassalam, Abyssinia
Distribution in Natal: Tete Pan (*leg.* Brown, 57, IZP 64.1.66), (Kuiper, 1966).

Range: Letaba River in Kruger National Park (Haas, 1936 as *P. costulosum.* According to Kuiper, 1964 this record refers to *pirothi*); eastern Transvaal, Egypt, southern Sudan, Mali, Uganda (Kuiper, 1966).

Pisidium costulosum Connolly, 1931. Rhenoster River at Rustfontein, Free State

Distribution in Natal: Widely distributed but not known to occur below 500 m (1,640 ft.), (Kuiper, 1966).
Range: Known from South Africa only, where it is recorded from Western Cape Province, Free State, and Transvaal (Kuiper, *loc. cit.*).

Pisidium langleyanum Melville & Ponsonby, 1891. Port Elizabeth

Distribution in Natal: Durban (Kuiper, 1964); widely distributed (Kuiper, 1966).
Range: Known from South Africa only, where it is recorded from Eastern Cape Province, and Transvaal (Kuiper, 1966.).

Pisidium viridarium Kuiper, 1956. Near Nairobi, Kenya

Distribution in Natal: Widely distributed from the coast to the foothills of the Drakensberg escarpment (Brown & Kuiper, unpublished observations).
Range: Western Cape Province, Basutoland, Rhodesia northwards to Ethiopia (Kuiper, 1964).

Pisidium ovampicum Ancey, 1890. Ovambonde, Ovamboland

Distribution in Natal: Stanger (Brown & Kuiper, unpublished observations).
Range: Western Cape Province, Uganda, Congo, Ethiopia (Kuiper, 1964); eastern Cape, eastern Transvaal, Swaziland (Brown & Kuiper, unpublished observations).

Eupera Bourguignat

Eupera ferruginea (Krauss, 1848). River Knysna, Cape Province

Distribution in Natal: Localities near the coast as far south as Illovo Lagoon (Connolly, 1939).
Range: Eastern Transvaal (Haas, 1936; Schutte & Frank, 1964); Southern Rhodesia (Connolly, 1939); Mozambique (Azevedo et al., 1961, as *E. crassa* Mandahl-Barth. According to Dr. Mandahl-Barth, pers. comm., this record refers to *E. ferruginea*).

Eupera parasitica (Deshayes, 1854). Upper Nile

Distribution in Natal: Tete Pan (*leg.* Brown, 57, IZP 64.1.66), Inyezane River north of Gingindlovu (*leg.* Brown, 383).
Range: Congo, Cameroon (Haas, 1936); Lakes Victoria and Albert (Mandahl-Barth, 1954).

Seven of the 10 forms newly recorded from Natal reach their southernmost limits, so far as is known, in this province: *Anisus coretus, Segmentorbis angustus, Lentorbis junodi, L. carringtoni, Caelatura framesi,* and *Eupera parasitica. P. viridarium* and *P. ovampicum*

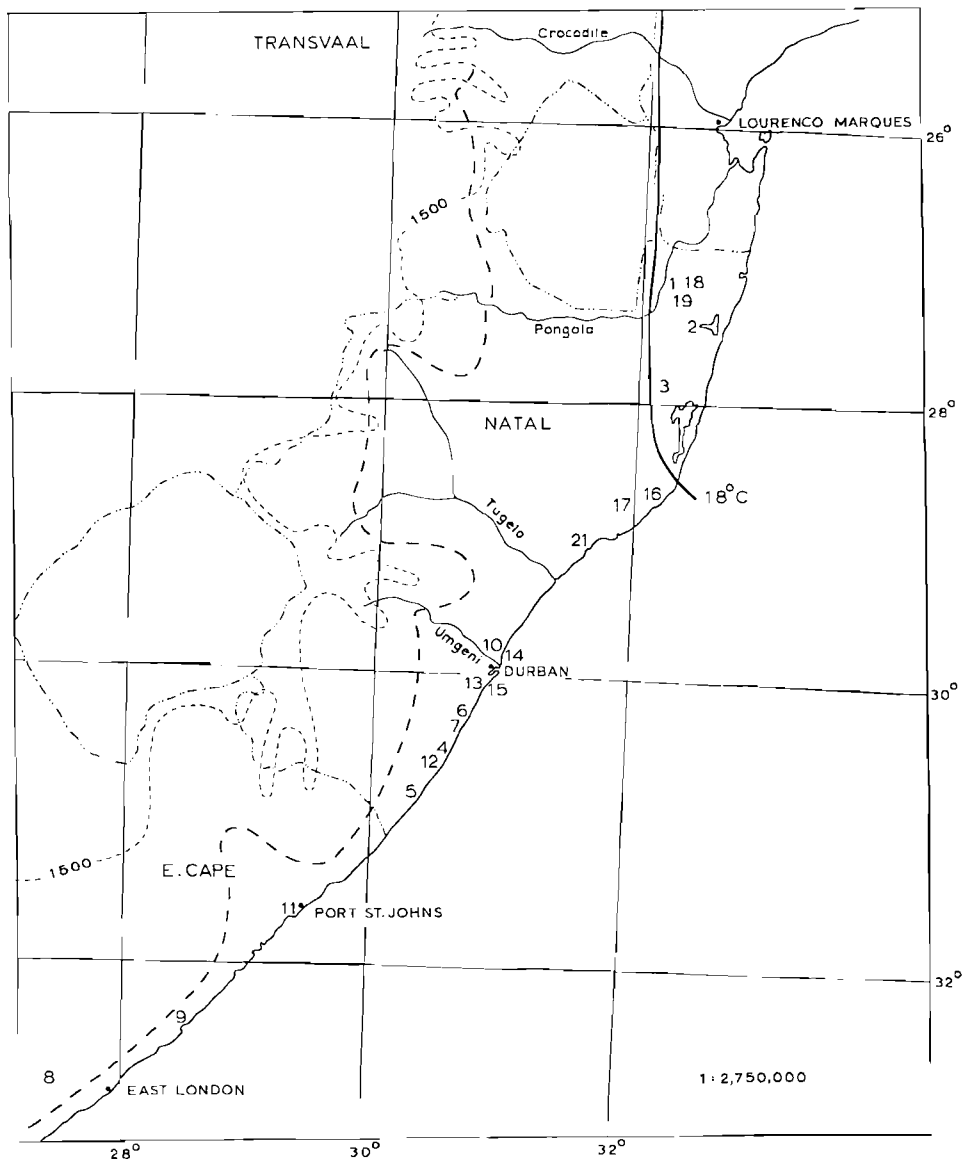
are extensively distributed in southern Africa and also occur in north eastern Africa. *Physa acuta* and *Helisoma* sp. have probably been introduced by human activities.

DISCUSSION

Distinctive elements in the terrestrial molluscan fauna of southern Africa have been made the basis of zoogeographical regions occupying the greater part of the continent south of latitude 20° (Germain, 1909; Pilsbry & Bequaert, 1927). The latter authors mentioned the freshwater operculate genus *Tomichia* among forms restricted to their South African Region but stressed, as did Germain, the homogeneity and 'uniformity over immense areas' of the African freshwater Mollusca. However, the molluscan fauna in freshwaters south of latitude 23° is actually far from homogeneous, including one group of forms with a strictly limited distribution mainly in the tropical climatic region. Their presence in the lowlands of eastern Transvaal and Natal contributes to the rich fauna of these areas. Similar tropical assemblages are known in other groups of animals, in some of which there are also assemblages having their centres of distribution in the temperate climatic region of Cape Province (e.g., Amphibia, Poynton, 1962 a & b and 1964; Dytiscidae, Omer-Cooper, 1962). In temperate South Africa the freshwater Mollusca are poorly represented in numbers of forms and none have been reported among the fauna endemic to the acid streams that are characteristic of the coastal region of western Cape Province (Harrison & Agnew, 1962).

For general discussion of the zoogeography of Africa the most useful climatic regions are those defined on the basis of the distributions of vegetation types, because many animals live in close association with plants. However, freshwater organisms are not directly dependent upon terrestrial vegetation, and Poynton (1964) has demonstrated that temperature criteria provide a convenient means of defining zoogeographic groups within the Amphibia. A tropical form may be defined (Poynton, *loc. cit.*) as one having at least a substantial part of its range within the area experiencing a tropical climate, i.e. enclosed by the 18° C, (64.4° F.) Mean July isotherm. Defined in this way the boundary of the tropical region extends from the western border of Mozambique to the southern end of Lake St. Lucia, enclosing the coastal plain of north eastern Natal (Map 1). The following molluscs which are tropical in the sense of Poynton have been recorded from this plain or its southward extension to the Tugela River (forms marked with an asterisk are not known to occur south of Lake St. Lucia): *Lanistes ovum**, *Bellamya capillata**, *Cleopatra ferruginea**, *Melanoides tuberculatus*, *Neritina natalensis*, *Biomphalaria pfeifferi*, *Gyraulus costulatus*, *Anisus coretus*, *Segmentorbis planodiscus*, *S. angustus*, *S. kanisaensis*, *Lentorbis junodi*, *Bulinus natalensis*, *B. forskali*, *B. africanus*, *B. globosus*, *Aspatharia wahlbergi**, *Caelatura framesi**, *Corbicula africana*, *Pisidium pirothi**, *Eupera ferruginea*, and *E. parasitica*. *Thiara vouamica*, *Neritina gagates*, *Septaria tessellaria* and *Lentorbis carringtoni* are also members of this group but have not been recorded from north of the Tugela River in Natal. The presence of *Sphaerium capense* in northeastern Natal and the eastern Transvaal sugggests that it should be included with the tropical forms but little is known of its distribution outside South Africa.

The ranges of some tropical freshwater molluscs extend to various distances outside the tropical climatic region in what may be termed subtraction areas where the number of tropical forms becomes progressively smaller with increasing distance from the tropical



Map 1. The southernmost known localities of tropical freshwater Mollusca in eastern South Africa. The extent of the westwards subtraction area is indicated by the western limits of *Bulinus africanus*, which with *B. forskali* extends further inland than the other tropical forms occurring in Natal.

———— 18°C. (64.4°F.) Mean July isotherm.
— — — Approximate western limits of *B. africanus*.
—·—·— International and provincial boundaries.
– – – – 1500 m (3,920 ft.) contour.

1: *Lanistes ovum;* 2: *Bellamya unicolor;* 3: *Cleopatra ferruginea;* 4: *Thiara vouamica;* 5: *Neritina natalensis;* 6: *N. gagates;* 7: *Septaria tessellaria;* 8: *Biomphalaria pfeifferi;* 9: *Gyraulus costulatus;* 10: *Anisus coretus;* 11: *Segmentorbis planodiscus;* 12: *S. angustus;* 13: *S. kanisaensis;* 14: *Lentorbis junodi;* 15: *Bulinus natalensis;* 16: *B. globosus;* 17: *Aspatharia wahlbergi;* 18: *Caelatura framesi;* 19: *Pisidium pirothi;* 20: *Eupera ferruginea;* 21: *E. parasitica;*

region. Many tropical forms reach their southernmost limits in the subtraction area extending down the Natal coast into eastern Cape Province (Map 1) but others continue southwestwards in a narrow coastal belt; a few have been recorded from apparently isolated localities in southern Cape Province at considerable distances from their main areas of distribution, for example *Melanoides tuberculatus* (Port Elizabeth), *Corbicula africana* (Swellendam), *Eupera ferruginea* (Knysna). Subtraction of tropical forms also takes place in the lowlands north of Natal; *Pila gradata* (Smith), *Lanistes ellipticus* von Martens, *Gabbia humerosa* (von Martens), *Cleopatra morelli* Preston, and *C. bulimoides* (Olivier) have not been recorded south of Mozambique, and *Melanoides victoriae* (Dohrn) and *Aspatharia petersi* (von Martens) occur in the eastern Transvaal (Oberholzer & van Eeden, in press) but are not known from Natal.

To the west of the tropical region the limits of freshwater molluscs extend furthest inland in river basins where climatic conditions are generally warmer than on the neighbouring highlands; a progressive decrease in distribution from north to south is illustrated by the range of *Bulinus (Physopsis) africanus* (Map 1). It is reasonably certain that *B. africanus* occurs further inland than *Biomphalaria pfeifferi*, and that prosobranchs and *Aspatharia* inhabit the lower altitudes only. This pattern of distribution is similar to that described for the Crocodile River system, south eastern Transvaal by Schutte & Frank (1964), but those authors reported the Ancylidae to be confined to higher altitudes, whereas in Natal *Burnupia* and *Ferrissia* occur at sea level.

The importance of the tropical element in the molluscan fauna of Natal freshwaters may be gauged from the fact that of the 56 forms indigenous to the province no more than 14 are known to occur in western Cape Province: *Lymnaea natalensis, Gyraulus lamyi, Anisus natalensis, Bulinus tropicus, B. diaphanous, B. corneus, B. forskali, Ferrissia connollyi, Cafferia caffer, Corbicula africana, Pisidium langleyanum, P. viridarium, P. costulosum* and *P. ovampicum*. On the other hand, 15 forms present in western Cape Province have not been recorded from Natal, namely *Tomichia spp., Bulinus tropicus* var. *verreauxii* (Bourguignat), 3 forms of *Burnupia*, and *Cafferia caffer verreauxi* (Küster). These may be found to constitute a small local assemblage when their taxonomy has been studied more fully. *Pisidium casertanum* also occurs in western Cape Province and has not been found in Natal, but this species is widely distributed in Africa and in the Holarctic regions.

It seems that temperature may play an important part in governing the ranges of tropical freshwater molluscs, as some species are restricted to the northern end of the Natal coastal plain although there are many apparently suitable habitats further south. It has previously been suggested that variation in the western limits of *Bulinus (Physopsis) africanus* in Natal may be in accordance with variation in temperature conditions associated with differences in altitude (van Eeden et al., 1965). The profound effect of temperature on survival and fecundity demonstrated experimentally by Shiff (1964) and Sturrock (1966) for *Bulinus (P.) globosus* and *Biomphalaria pfeifferi* supports the view that temperature may exert a direct effect on the distribution of these and other species. Poynton (1962 & 1964) believes temperature to play an important part in limiting the ranges of tropical amphibians but points out that the existing temperature gradient down the Natal coast is unlikely to be responsible for the concentration of their southern limits in the vicinity of Lake St. Lucia; this, he suggests, may be the result of repeated expansions and retractions of ranges in

response to climatic changes. It is to be expected that the ranges of freshwater molluscs also fluctuate with climate, with the consequence that isolated populations of tropical forms in southern Cape Province may be either relicts are pioneers, but the Lake St. Lucia region does not appear to be of particular significance as a southern limit (Map 1). While the general pattern of distribution shown by tropical freshwater molluscs in south eastern Africa may be attributed with some confidence to the present and past effects of temperature, the local distribution of a particular species at the fringe of its range may not be due simply to its temperature tolerance but also to competition from forms adapted to cooler conditions.

Leaving aside species considered above to be tropical, the genera *Burnupia* and *Ferrissia*, and the rare endemic species *Tomichia natalensis*, we may divide the remaining indigenous freshwater molluscs of Natal into 2 groups. Firstly, species present in tropical Africa and also in so great a part of the temperate region of southern Africa that they seem to be not comparable to the other tropical forms: *Lymnaea natalensis*, *Anisus natalensis*, *Bulinus tropicus*, *Pisidium viridarium* and *P. ovampicum*. Secondly, species which are apparently restricted to southern Africa where they occur predominantly in the temperate region: *Gyraulus lamyi*, *Cafferia caffer*, *Pisidium langleyanum* and *P. costulosum*. *Lymnaea truncatula* has also been reported most frequently from the temperate region of southern Africa, but it is doubtfully indigenous; according to Hubendick (1951) its distribution in Africa is suggestive of introduction by migratory birds, but this snail appears to have had a considerable history in at least Bechuanaland where subfossil shells have been found (Connolly, 1939).

There should be little doubt that *Physa acuta*, *Lymnaea columella*, and *Helisoma* sp. have been introduced, probably by human activities, into Natal and other parts of southern Africa within the last few decades for none of them has been reported from the extensive collections of freshwater molluscs made in South Africa early in the present century. *Biomphalaria angulosa* is also believed to have been introduced into South Africa (van Eeden, 1966). *Lymnaea columella* has proved to be the most successful colonist among these alien species.

The absence of large mussels of the family Mutelidae from much of Natal and the entire southern tip of Africa should be considered in connection with the assertion by McMichael & Iredale (1959) that the presence of this family in Africa, Australia, and South America could be explained by 'a southern distribution across a temperate antarctic land mass'. In this case the Mutelidae in Africa have followed a course of ecological evolution that has enabled them to invade the tropical region but has resulted in their disappearance from the southern temperate region. A northern origin of the African mutelids is perhaps more likely, and is also probable for limpets of the genus *Ferrissia* because forms which may be classified in the subgenus *F.* (*Pettancylus*) on the basis of their anatomy occur in Natal, India and Australia (Brown, 1967).

A comprehensive analysis of the biogeography of the freshwater Mollusca of Natal will depend upon the results of future taxonomic revisions embracing far greater areas of Africa, but it seems that the distinction discernible at present between tropical and other forms will continue to be valid. The apparently wide ecological tolerance of *Lymnaea natalensis* and other abundant forms with ranges of comparable area is perhaps due to the production of locally adapted races in which self-fertilisation may play an important part

in the conservation of successful genotypes. One objective of the taxonomist will be to define the distributions of local races.

SUMMARY

Sixty forms of recent Mollusca from freshwaters in Natal Province, South Africa are listed with brief summaries of their distributions in the province and ranges in Africa. Ten forms are newly recorded for Natal of which 6 are not known to occur south of this province, namely *Anisus coretus*, *Segmentorbis angustus*, *Lentorbis junodi*, *L. carringtoni*, *Caelatura framesi* and *Eupera parasitica*. *Pisidium viridarium* and *P. ovampicum* are widely distributed in southern and central Africa, and *Physa acuta* and *Helisoma sp.* have probably been introduced by human activities in recent time.

One group predominant in north eastern Natal comprises 26 forms that may be termed tropical because substantial parts of their ranges lie within the tropical climatic region defined on the basis of temperature, although some of them extend outside the tropical region into subtraction areas to the south and west. The distribution patterns of the tropical forms support the idea that occurrence is governed to a considerable extent by the influence of temperature; some of those that occur exceptionally far south are distributed in apparently isolated populations which might be regarded as relicts or pioneers.

Also present in Natal are 5 forms distributed mainly in the temperate region of southern Africa, and 5 which are distributed in the tropical and the temperate regions. The molluscan fauna of freshwaters in the temperate region of southern Africa is not comparable in diversity to that of the tropical region, and consequently the number of forms recorded from north eastern Natal is much greater than from western Cape Province which is a rich centre of endemism for some other groups of organisms.

The mutelid mussels are represented in Natal by the genus *Aspatharia* with a tropical distribution pattern, which indicates a northern origin for this family in Africa. A northern origin is also probable for limpets of the subgenus *Ferrissia* (*Pettancylus*).

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